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NUTRITIONAL HABITS OF THE NOCTULE BAT *NYCTALUS NOCTULA* (SCHREBER, 1774) IN SWITZERLAND

Sandra Gloor, Hans-Peter B. Stutz, Vincent Ziswiler

Abstract: During one season (from April to November 1989) faecal pellets of the Noctule bat *Nyctalus noctula* were collected in three roosts in buildings in villages. At seven roosts in trees in the town of Zürich, Noctule bats were caught every two weeks from April to November and faecal pellets are collected. The faecal pellets are analysed both in terms of quality and quantity and compared from a regional and seasonal point of view.

Nyctalus noctula preferably feeds on Trichoptera and Diptera (Chironomidae, Anisopodidae, Tipulidae). These insects fly in swarms so the Noctule bat can hunt and catch a lot of prey in very short time: this can be termed filter feeding. It is surprising, that the Noctule bat with its powerful and strong theeth hunts such soft and small insects. In spring and autumn, though, when larger insects, such as Coleoptera (e. g. Melolontha sp. in spring, Geotrupes sp, in autumn) are frequent and swarming insects (e. g. Trichoptera) are rare, the larger insects are also hunted by the Noctule bat, a fact that points to an opportunistic hunting strategy.

Key words: *Nyctalus noctula*, faeces analysis, diet, foraging strategy.

Introduction

The Noctule bat *Nyctalus noctula,* a rather large and fast flying vespertilionid, is one of the most common bat species, distributed all over Europe except Scotland, Ireland and northern Scandinavia. It is known to migrate seasonally over large distances up to more than 1000 km (**Roer** 1977, **Heise & Schmidt** 1979).

In Switzerland and the southern part of Germany *Nyctalus noctula* does not nurse, but mates and hibernates there (**Gebhard** 1983, **Stutz & Haffner** 1986a, **Kronwitter** 1988). Its roosts are mostly found in hollow trees, but roosts can also be situated in crevices of buildings.

The present study tries to draw conclusions concerning the diet of this large bat species with the help of faecal analysis. Based on a comparison between the aerial insect fauna light trapped in a foraging area and the diet of *N. noctula* we will discuss its hunting strategy. The diet of the Noctule bat and the biology of the prey found in the faeces refer to the foraging strategy as well and point to different foraging habitats of *N. noctula*.

Methods

Study area: The faeces analysed in the present study were sampled in one town and three villages in the Swiss "Mittelland". The four places are situated in the north of the Alps, at a distance of no more than 23 km from Zürich (47° 20 'N 8° 35 'E), at an altitude between 410 to 500 metres above sealevel. Faeces were collected from March to November 1989.

Faeces sampled from buildings: Bat droppings were sampled from three roosts in buildings in the villages of Bremgarten, Rüti and Muri. The faeces fell down from the roosts onto the windowsills underneath the roosts. The droppings were sampled from 26th March to 18th November every two weeks (**sampling periods**). The roost in Muri was only found on 17th June. From this roost droppings were collected during the first week of the months of July, August, September and October. There were no Noctule bats present in the roost of Bremgarten from 21st May to 27th August, in the roost of Rüti from 3rd June to 7th July. Altogether 24 samples of faeces were stored for analysis.

Faeces sampled of individual bats from tree roosts in the town of Zürich: Noctule bats were trapped at eight different tree roosts in Zürich when they left their roosts in the evening. Trapped bats were placed separately in small boxes for an hour and then released. Faeces voided by the bats were removed from the boxes and stored for analysis. Because only few faecal pellets could be collected by this method (faecal pellets of 218 individuals, 37 % of all trapped Noctule bats), the sampling season was divided into three **sampling phases** of eight weeks (Phase I: 24th April to 18th June; phase II: 19th June to 13th August; phase III: 14th August to 18th October). The faeces from Zürich were then analysed for the three sampling phases.

No female Noctule bats were trapped from 9th June to 16th August. As the faeces of females and males were sampled separately, there were five samples of faeces from Zürich.

Ten Noctule bats were trapped in nylon mist nets in a foraging area in Zürich and treated like the bats trapped at tree roosts. The faeces of mist netted bats were only qualitatively analysed.

From the 29 faeces samples 15 faecal pellets each were analysed (a total of 435 pellets). Every pellet was placed in water and examined under a binocular for clearly recognizable diagnostic fragments of prey. The fragments were identified by reference to a key (**Chinery** 1986) or by comparing the fragments to a collection of insects of the area.

The abundance of a particular prey category was expressed as the **percentage occurrence** (% 0) (**Korschgen** 1971, **McAney** 1991). This percentage is calculated by taking the number of occurrences of the prey category divided by the number of droppings analysed, multiplied by 100. The sum of the values exceed 100 %, unlike the percentage frequencies in the results of the insect light trapping samples. The prey categories were not expressed as percentage volume because a large part of the dropping contents could not be identified and classified at all. Thus we decided not to work with the concept of volume.

Insect light trapping: To sample the aerial insect fauna an insect light trap was placed in a foraging area of the Noctule bat at the banks of a 20m-wide river in Zürich. In this foraging area a large part of the Noctule bats of Zürich forage during the first hunting

Table 1: Arthropoda found in faeces of *Nyctalus noctula* in the present study and in the studies of other authors.
References: (1) **Barrett-Hamilton & Hinton** 1910, (2) **Poulton** 1929, (3) **Cranbrook & Barrett** 1965, (4) **Howes** 1974, (5) the present study. so = suborder, sf = superfamily.

class	order	so	sf	family	genus	species	references
Arachnida							4, 5
	Araneidae			Araneae	*Amaurobius*	*Amaurobis atropos*	4
				Lycosidae	*Lycosa*		4
Insecta							1, 2, 3, 4, 5
	Ephemeroptera						5
	Saltatoria			Gryllidae	*Acheta*	*Acheta domestica*	3
	Hemiptera	Heteroptera		Corixidae			5
		Homoptera	Aphididea				5
	Neuroptera			Hemerobiidae	*Megalomus*	*Megalomus hirtus*	5
				Chrysopidae	*Chrysopa*		5
	Coleoptera						1, 2, 4, 5
				Rhizophagidae	*Rhizophagus*	*Rhizophagus poitus*	4
				Scarabaeidae			2, 4, 5
					Serica	*Serica brunnea*	4
					Melolontha		1, 2, 4, 5
						Melolontha vulgaris	2
					Aphodius		5
					Geotrupes		2, 5
						Geotrupes stercorarius	2
				Carabidae			4, 5
					Cychrus		5
					Abax	*Abax ater*	5
					Carabus		5
				Curculionidae	*Liophloeus*	*Liophloeus tessulatus*	4
	Diptera						4, 5
		Nematocera					4, 5
				Bibionidae	*Bibio*	*Bibio pononae*	4
				Chironomidae			5
				Trichoceridae			5
				Culicidae			5
				Tipulidae			5
				Anisopodidae	*Sylvicola*		5
		Brachycera					5
		Cyclorrhapha					4, 5
				Scatophagidae	*Scatophaga*	Scatophaga stercoraria	4
					Lyciella		4
	Trichoptera			Hydropsychidae			5
	Lepidoptera						1, 4, 5
	Hymenoptera						2, 4, 5
				Formicidae			2

period in the evening (**Bontadina et al.** unpupl. data). Light trapping took place during this first foraging period (**Stutz & Haffner** 1989b) for 90 minutes, every four weeks from 11th April to 2nd November. The light trap consisted of two daylight fluorescent tubes (OSRAM, L 18 W/10) and two fluorescent tubes with a higher rate of ultraviolet light (Sylvania, Lifeline, F 20 W/GRO). The insects were preserved in 70 % ethanol and identified by reference to the key of **Chinery** (1986).

Results

The prey categories found in the faecal pellets of *N. noctula* are a distribution of 2 classes, 8 orders and 11 families, 8 geni and 2 species (Table 1).

In the droppings from all the roosts over all sampling phases Trichoptera (48 %), Diptera (46 %) and Lepidoptera (28 %) were most frequently found. Coleoptera (18 %), Ephemeroptera (9 %), Hemiptera (3 %) and Arachnida (1 %) were less frequently present (Fig. 1).

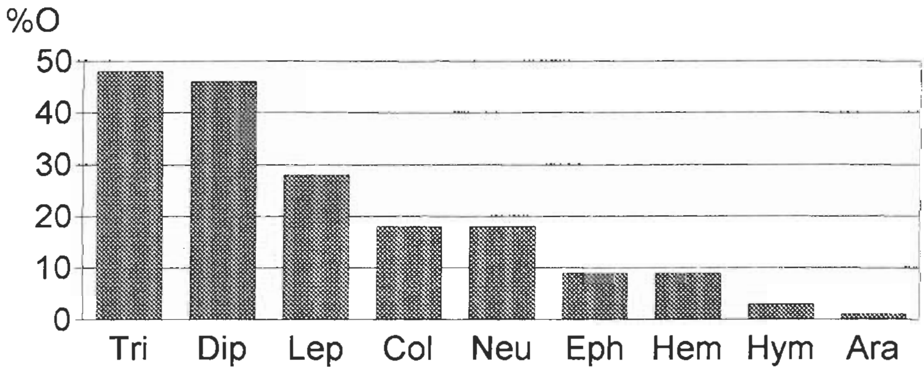

Fig. 1: Percentage occurrences (% 0) of the identified prey categories in the faeces from all places from 24th April to 8th October.

(Tri) Trichoptera, (Dip) Diptera, (Lep) Lepidoptera, (Col) Coleoptera, (Neu) Neuroptera, (Eph) Ephemeroptera, (Hem) Hemiptera, (Hym) Hymenoptera, (Ara) Arachnida. The data is equally weighed according to the three sampling phases.

By comparing the distribution of the prey of the four sampling places, it clearly shows, that the results of Zürich, Bremgarten and Muri are more or less similar, but differ from the results of Rüti (Fig. 2). This can be best shown by the prey that was most frequently identified, by the orders Trichoptera and Diptera. In Rüti Diptera predominated (72 %) and Trichoptera were much less present (3 %), whereas in the three other places, Trichoptera predominated (Zürich: 76 %, Bremgarten: 87 %, Muri: 66 %). Diptera, on the other hand, were less frequent (Zürich 17 %, Bremgarten 27 %, Muri 37 %).

In the qualitatively analysed faeces collected from mist netted bats only prey of one single category could be found in the faeces of the same date, e.g. Chironomidae or Trichoptera.

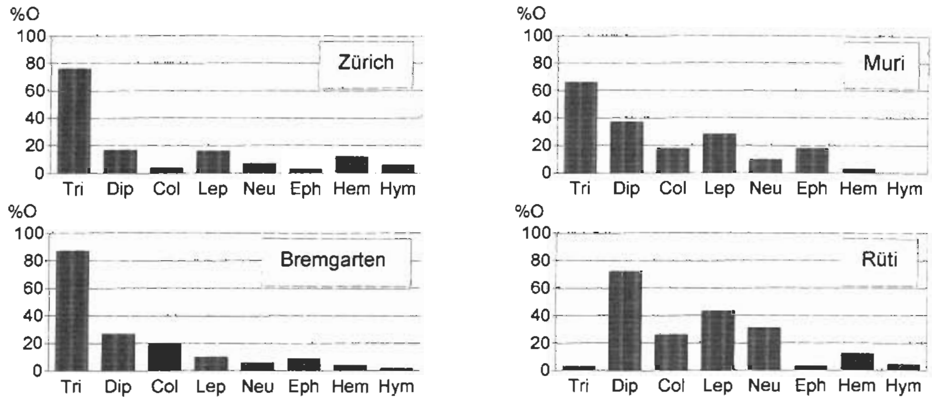

Fig. 2: Percentage occurrences (% 0) of the identified insect orders in the faeces from the four places from 24th April to 8th October.
(Tri) Trichoptera, (Dip) Diptera, (Lep) Lepidoptera, (Col) Coleoptera, (Neu) Neuroptera, (Eph) Ephemeroptera, (Hem) Hemiptera, (Hym) Hymenoptera, (Ara) Arachnida. The data is equally weighed according to the three sampling phases.

In the droppings from Zürich, Bremgarten and Rüti, the Diptera suborder Nematocera predominated and the suborders Brachycera and Cyclorrhapha were less frequently present. For the Diptera captured by light trapping this is even more evident. In the droppings from all the four places Chironomidae predominated over the other identified Nematocera families, just like the results of light trapping have shown (Table 2). In the faecal pellets with typical fragments of wing of Chironomidae the typical antennae of male Chironomidae could always be found as well. Female antennae were not present.

Two **Coleoptera** families could be found in the analysed faeces: Scarabaeidae and Carabidae (Table 3). Carabidae were only present in the droppings from Bremgarten (Table 4). In spring, the Scarabaeidae genus Melolontha predominated, whereas in autumn the geni Aphodius and Geotrupes predominated.

Table 2: Percentage frequencies of Diptera found in the faeces from Rüti, Bremgarten, Muri and Zürich and of Diptera captured by light trapping.
Suborder Nematocera (**Nem**), suborder Brachycera und Cyclorrhapha (**Bra & Cyc**), not identified Diptera (**not ident. Diptera**), Chironomidae (**Chi**), Anisopodidae (**Ani**), Tipulidae (**Tip**), other Nematocera families (**other Nem**).

places of faeces sampling	**Nematocera**					**Bra & Cyc**	**not ident. Diptera**
	Chi	Ani	Tip	other Nem	Nem total		
Rüti	74	2	14	—	90	2	8
Bremgarten	23	6	19	—	48	8	44
Muri	13	10	5	—	28	36	36
Zürich	26	20	18	—	64	15	21
Light trap Zürich	65	1	0	29	95	4	—

Table 3: Percentage occurences of the Coleoptera identified for the sampling phases in the faeces of all four sampling places.
The results of the four sampling places are equally weighed. Scarabaeidae (**Sca**), Carabidae (**Car**), Melolontha (**Mel**), Aphodius (**Aph**), Geotrupes (**Geo**), Pterostichinae (**Pte**), Cychrus (**Cyc**).

sampling phase	Coleoptera total	Scarabaeidae				Carabidae		
		Mel	Aph	Geo	**total**	**total**	Pte	Cyc
I	31	18	1	1	**21**	—	—	—
II	10	1	—	—	**2**	—	—	—
III	13	—	5	2	**7**	**2**	1	1

Table 4: Percentage occurrences of the Coleoptera identified in the faeces from Bremgarten according to the two week-sampling periods.
Scarabaeidae (**Sca**), Carabidae (**Car**), all the Coleoptera (**Col total**), Melolontha (**Mel**), Aphodius (**Aph**), Geotrupes (**Geo**), Pterostichinae (**Pte**), Cychrus (**Cyc**), Abax (**Aba**), Carabus (**Car**).

sampling-period	**Sampling phase**	**Col total**	**Scarabaeidae**				**Carabidae**				
			Mel	Aph	Geo	**total**	**total**	Pte	Cyc	Aba	Car
11th—25th Apr		**33**	13	7	—	**27**	—	—	—	—	—
— 7th May	I	**80**	33	—	—	**40**	—	—	—	—	—
—21st May		**27**	7	—	—	**7**	—	—	—	—	—
28th Aug — 9th Sep		**13**	—	—	—	—	—	—	—	—	—
—23rd Sep	III	**13**	—	7	—	—	—	—	—	—	—
—16th Oct		**33**	—	—	20	**20**	**20**	7	13	—	—
—21st Oct		**60**	—	7	13	**13**	**47**	20	7	13	7
— 4th Nov		**40**	—	—	7	**7**	**13**	7	7	7	7
—18th Nov		**33**	—	7	7	**20**	**7**	—	—	—	—

Two **Neuroptera** families were identified: Hemerobiidae and Chrysopidae. In the faeces from Zürich, Bremgarten and Muri Hemerobiidae could be found just as often as Chrysopidae, whereas in the faeces from Rüti Chrysopidae were present in 62 % and Hemerobiidae in 38 % of the droppings. By light trapping only Chrysopidae were captured.

Most of the identified **Hemiptera** were Heteroptera. Only in three cases Aphididea were identified: in the droppings from Zürich in the 2nd sampling phase (19th June to 13th August), in the droppings from Muri in the 8th sampling period (2nd to 16th July).

By light trapping in a foraging area of the Noctule bat in Zürich the same insect orders were captured as found by faecal analysis. The following insect taxa were identified by faecal analysis but not captured by light trapping: Corixidae (Heteroptera), Hemerobiidae (Neuroptera), Scarabaeidae and Carabidae (Coleoptera) and Culicidae (Diptera). Diptera predominated in the insect samples of the first three and the last two trapping nights, whereas Trichoptera extremely predominated in the samples of 12th

July, 9th August and 6th September. The total number of captured insects was particularly high on 12th July (Fig. 3 a). The occurrence of Lepidoptera was no higher than 4 % over the eight nights of trapping, other insecta orders represented no more than 2.5 % of all captured insects.

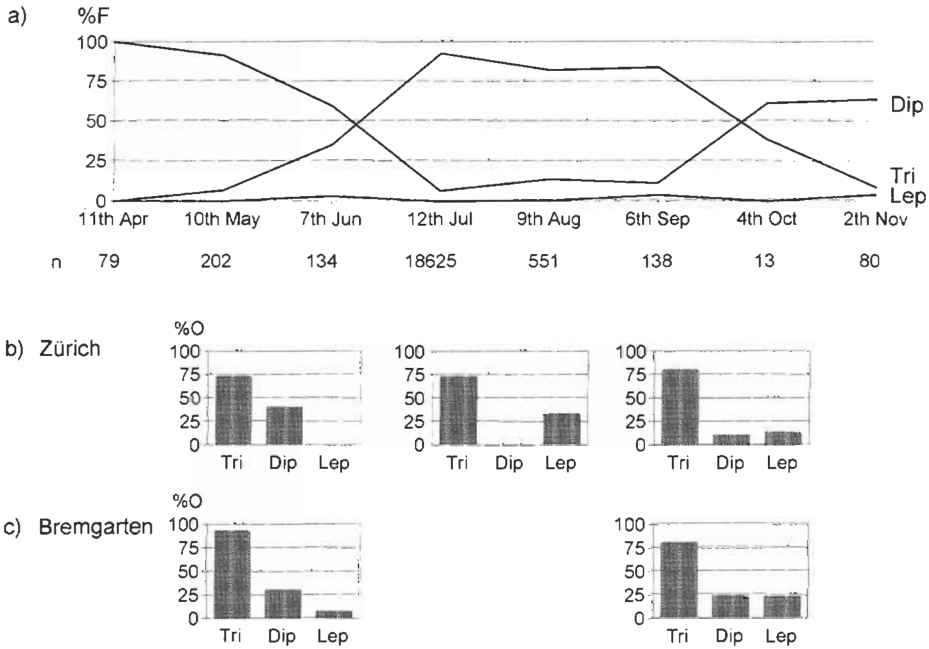

Fig. 3: (a) Percentage frequencies of the abundance of Trichoptera, Diptera and Lepidoptera in a foraging area in Zürich, (b) percentage occurrences (% 0) of Trichoptera, Diptera and Lepidoptera in the faeces from Zürich and (c) in the faeces from Bremgarten.
n = total number of captured insects. (Dip) Diptera, (Tri) Trichoptera, (Lep) Lepidoptera.

Figure 3 shows the percentage frequencies of insects captured by light trapping for the eight trapping nights and the percentage occurrences of Trichoptera, Diptera and Lepidoptera in the faeces of Zürich and Bremgarten for the three sampling phases. The roost of *N. noctula* in Bremgarten was situated near the bank of a river like the roosts in Zürich. That is the reason why the results from Bremgarten are also taken into account when compared with the abundance of the three insect orders in the foraging area of Zürich.

In the faeces from Zürich and Bremgarten Trichoptera predominated in all the three sampling phases, but in the faeces from Bremgarten in the first sampling period (1st to 25 th April) Diptera were present in 67 % and Trichoptera in 40 % of the droppings. These findings are similar to the results of the light trapping samples. In the faeces from Zürich, Diptera are just present in spring and autumn, in the seasons when Diptera were relatively frequent.

Discussion

The methods of faecal analysis and insect light trapping

Faecal analysis is a reliable technique to examine the diet of insectivorous bats (**Kunz & Whitaker** 1983, **Whitaker** 1988). However, as there are a few uncertainties, the method can be a source of bias in the results (**Rabinowitz & Tuttle** 1982). Prey items such as wings, legs and antennae are often discarted. Fragments of large and hard prey are more often discted than fragments of small and soft prey (**Coutts et al.** 1973). As a result large and hard prey is generally given too much weight. On the other hand, solid structures such as legs or jaws remain recognizable even after having been chewed and swallowed, whereas soft bodied insects may have been almost completely digested or splitted into small fragments, leaving little identifiable remains in the faeces (**Yalden & Morris** 1975).

The different methods used to sample the faecal pellets could be another source of bias. The faeces from Bremgarten, Muri and Rüti should give a complete picture of the diet of *N. noctula*, because after foraging the Noctule bat returns for digestion into the roost (**Kronwitter** 1988). The results of the analysis of faeces from Zürich, however, should be examined with caution. The faeces were sampled in the evening from bats trapped while they were leaving their roosts. Their droppings only contained those prey fragments that had not been voided during the day.

Accurate assessment of the availability of aerial insects is a great problem. A lot of different techniques are suggested (**Kunz** 1988). **Johnson & Taylor** (1955), **Buchler** (1976) and **Swift et al.** (1985) worked with different suction traps, **Rydell** (1989) tried to sample the aerial insect fauna by a hand net whereas **Black** (1974) and **Jones** (1990) used light traps just to mention a few examples.

The method of light trapping allows quantitative and qualitative conclusions about the abundance of different insect categories (**Taylor & Carter** 1961). There are a few problems, however, e. g. because there are some insect categories that are more strongly attracted by the light traps than others (**Jermy** 1974, **Rezbanyai** 1977). The Noctule bat is known to begin to hunt just after sunset. **Williams** (1935, 1939) though, suggested starting light trapping not before half an hour after sunset. In the present work aerial insects were sampled only during the first foraging period of the Noctule bat, but *N. noctula* often leaves its roosts more than once a night depending on temperature and weather (**Stutz & Haffner** 1986b, **Kronwitter** 1988, **Rachwald** 1992).

The Noctule bat uses more than one foraging area a night (**Kronwitter** 1988). However, a large part of the Noctule bats from the roosts in Zürich seem to forage in the light trapping area during the first foraging period (**Bontadina et al.** unpubl. data).

There were almost no Coleoptera captured by the light trap. Because Coleoptera are considerably frequent in the faeces, their availability ought to be sampled with another technique.

The diet of the Noctule bat

Until now there are no detailed studies of prey selection by *N. noctula.* Earlier studies were based on observations made by chance or on small quantities of not systematically sampled faeces. According to **Barrett-Hamilton & Hinton** (1910) *N. noctula* feeds on Coleoptera, Lepidoptera and also smaller insects. The results of the observations published by **Poulton** (1929) and the study of **Kolb** (1958) confirm the above. **Cranbrook & Barrett** (1965) described observations of Noctule bats hunting house crickets (Gryllidae: *Acheta domestica*) over a municipal rubbish tip.

Howes (1974) collected faecal pellets, which fell down from a tree roost while the Noctule bats were leaving. He identified Aranea and other non-flying organisms in the faeces and concluded, that the Noctule bat might forage on the ground. The present study does not support this conclusion. All the insect taxa identified in the faeces have representative species which are able to fly, even the Carabidae genus Carabus. The Arachnida found in the droppings were just a small part of all the prey. Arachnida cannot fly but they do not have to be gleaned from the ground or from foliage. They can hang into the flying paths of the Noctule bat and may be caught by chance. The faecal pellets collected by **Howes** (1974) need not be pellets only of *N. noctula*, because the same tree holes can be inhabited by *N. noctula, Myotis daubentoni* or *N. leisleri* (**Cerveny & Bürger** 1987).

Foraging habitats

The results of the faecal analysis point to similar foraging habitats in Zürich, Bremgarten and Muri and to a different foraging habitat in Rüti. The same tendencies can be shown by comparing the faecal analysis with the availability of the aerial insect fauna.

The biology of prey present in the faeces also refers to foraging habitats. Trichoptera predominated in Zürich, Bremgarten and Muri. These insects indicate foraging habitats near rivers or lakes, because the larvae of Trichoptera develop in water only and imagines usually do not fly far away from the river or lake where they developed (**Chinery** 1986). The larvae of the Diptera present in the faeces also mostly develop in water but there are Diptera families present in the faeces that are known not to develop in water, as well. The prey most strictly connected with water are the Ephemeroptera. They make just a small part of the diet of the Noctule bat in Rüti and Zürich, whereas im Bremgarten and Muri they are temporarily quite frequent in the faeces.

Based on these results we suggest, that the foraging habitats in Zürich, Bremgarten and Muri are — at least partly — situated near stretches of water, whereas the foraging habitats in Rüti are not. Studies in Bremgarten (**Haffner & Stutz** 1989), Muri (**Beck** pers. com.) and Zürich (**Bontadina et al.** unpubl. data) confirm this suggestion. There are no known observation of hunting Noctule bats in Rüti, but there are no large rivers or lakes near this village. The Noctule bat seems to be able to hunt in different foraging habitats and is not restricted to foraging areas near stretches of water.

Hunting strategy

According to many authors *N. noctula* belongs to the group of open-air foragers. These fast flying bats feed on the wing exclusively and are perhaps restricted in the selection of the size of prey items they can efficiently manipulate and eat (**Black** 1974). Depending on the information contents of the echo, they might respond differently to aggregations or swarms of insects (**Webster & Brazier** 1965 in **Black** 1974). Predators of swarming insects can hunt and catch a lot of prey in very short time. This can be termed as filter feeding (**Ross** 1967) and may be related to an opportunistic hunting strategy.

Many of the prey taxa present in the faeces fly in swarms, often over waters. The Trichoptera (**Chinery** 1974), the Diptera families Chironomidae (**Chinery** 1986) and Anisopodidae (**Brauns** 1964) and the Neuroptera families Hemerobiidae and Chrysopidae (**Aspöck et al.** 1980) belong to these insects. Tipulidae can also temporarily appear in large numbers (**Service** 1973). The swarms of some of these insects are so-called mating swarms of male insects among which females are relatively rare. In fact *N. noctula* seems to forage in such mating swarms, as in the faeces with Chironomidae fragments of male antennae of Chironomidae were present and female antennae were absent.

All the above mentioned prey belongs to middle sized or small insects. This is surprising, because the Noctule bat is a large bat with strong and powerfull teeth, at least for European circumstances. This enables the Noctule bat to eat rather big and hard insects (**Lutz** 1985, **Stutz** 1987). In fact also big and solid prey was found in the faeces: Melolontha, Geotrupes and Heteroptera. These insects which can also occur in large numbers were eaten at times when the total number of flying insects was generally rather small (spring and autumn), which can also be demonstrated by the results of light trapping. At such times it could be important to *N. noctula* to be able to hunt big, mostly individually flying insects, as well. This is once more indicative of an opportunistic foraging strategy.

Conclusions about the foraging strategy are only possible when comparing between the availability of prey and the diet of the predator. The comparisons in the present paper which are only possible with certain reservations point to an opportunistic foraging strategy at least as far as Diptera, Trichoptera and Lepidoptera are concerned. This hypothesis needs to be verified with the help of further studies.

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Authors' address:

Ms. Sandra Gloor
Eichstraße 14
CH-80[illegible]ürich
Switzerland

Mr. Hans-Peter B. Stutz & Mr. Vincent Ziswiler
Zoologisches Museum, Universität Irchel
Winterthurerstraße 190
CH-8057 Zürich
Switzerland